

Folk Explanations of Behavior: A Specialized Use of a Domain-General Mechanism



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Abstract

People typically explain others' behaviors by attributing them to the beliefs and motives of an unobservable mind. Although such attributional inferences are critical for understanding the social world, it is unclear whether they rely on processes distinct from those used to understand the nonsocial world. In the present study, we used functional MRI to identify brain regions associated with making attributions about social and nonsocial situations. Attributions in both domains activated a common set of brain regions, and individual differences in the domain-specific recruitment of one of these regions—the dorsomedial prefrontal cortex (DMPFC)—correlated with attributional accuracy in each domain. Overall, however, the DMPFC showed greater activation for attributions about social than about nonsocial situations, and this selective response to the social domain was greatest in participants who reported the highest levels of social expertise. We conclude that folk explanations of behavior are an expert use of a domain-general cognitive ability.

Keywords

social cognition, neuroimaging, semantic memory, theory of mind, causality, open materials

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Psychologists and laypeople all desire explanations for human behavior. Whereas psychologists' efforts to explain behavior demand years of formal training, laypersons' efforts seem to demand no formal training at all. In fact, most 3-year-old children already have the ability to produce culturally acceptable explanations of other people's behavior (Bartsch & Wellman, 1989). This fundamental aspect of human social cognition has been the object of theories and research in disciplines ranging from social psychology (Fiske & Taylor, 1984; Heider, 1958) to developmental psychology (Gopnik & Schulz, 2004) to the philosophy of mind (Davidson, 1963; Dennett, 1989). These disciplines largely converge on the view that folk explanations of human behavior are the product of a cognitive ability that is distinct from the one used to explain nonsocial events of a natural origin. In the research reported here, we used functional MRI (fMRI) in conjunction with a novel behavioral task to examine the idea that folk explanations of behavior require specialized cognition.

Lay explanations of human behavior usually rest on attributing a person's observable behavior to an inferred

mental state, such as their motive or belief about the behavior (Davidson, 1963; Dennett, 1989; Malle, 2004). These causal attributions draw on what has been variously termed a *folk psychology* or *theory of mind*, that is, a culturally shared conceptual framework that specifies the meaning of mental terms, both as they causally relate to each other (e.g., anger causes aggression) and to observable behaviors (e.g., embarrassment causes blushing; Apperly, 2012; Bartsch & Wellman, 1989; Malle, 2004). Thus, folk psychology provides a powerful conceptual framework for making attributions about the social world (Heider, 1958; Heyes & Frith, 2014). For attributions about changes observed in the physical world, however, folk psychological concepts are much less powerful. Such changes are best understood using a different set of concepts that describe (either lay or scientific) laws of nature (Dennett, 1989).

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Thus, attributions about social and nonsocial situations clearly demand the use of different domains of causal knowledge. However, it remains unclear whether they also require distinct cognitive processes operating on that knowledge. In prior work, we have shown that attributions about human behavior selectively activate an anatomically well-defined left-hemisphere brain network that prominently includes regions of the medial and orbitofrontal prefrontal cortex, precuneus, temporoparietal junction (TPJ), and anterior superior temporal sulcus (aSTS; Spunt & Adolphs, 2014; Spunt, Falk, & Lieberman, 2010; Spunt & Lieberman, 2012a, 2012b; Spunt, Satpute, & Lieberman, 2011). By exclusively focusing on attributions about human behavior, these studies could not examine an important unanswered question: Does this network implement an attributional process that is domain general or one that is specifically tied to the social domain?

Work in social neuroscience suggests that the functions of this network might be specific to the social domain. It has long been known that psychiatric illness and brain lesions can cause dramatic changes in social cognition while sparing ostensibly domain-general executive functions (Leslie & Thaiss, 1992; Samson, Apperly, Chiavarino, & Humphreys, 2004). Similarly, numerous neuroimaging studies suggest that brain regions supporting social judgments dissociate from those that support similar nonsocial judgments (Kennedy & Adolphs, 2012; Mitchell, 2009; Van Overwalle, 2011). However, because these studies have typically relied on directly comparing responses to social stimuli with responses to nonsocial stimuli (e.g., Martin & Weisberg, 2003; Mason, Magee, Kuwabara, & Nind, 2010; Mitchell, Heatherton, & Macrae, 2002; Mitchell, Macrae, & Banaji, 2005), their findings could be, in part, driven by domain-specific expertise, attention, and motivation—factors that might lead the social domain to place relatively stronger demands than the nonsocial domain on cognitive processes that are intrinsically domain general (Grelotti, Gauthier, & Schultz, 2002; Tarr & Gauthier, 2000). To address this possibility, we used fMRI in conjunction with a novel behavioral task that allowed attributional processing to be isolated within each domain separately.

Method

Participants

Twenty-one adults from the Los Angeles metropolitan area participated in the study. Two individuals were excluded after they participated, 1 because we discovered that the individual had an incidental brain abnormality, and the other because of a recruitment-screening error. This left 19 participants for the analysis (13 males,

6 females; mean age = 28.32 years, range = 21–46). Sample-size determination was based on the first author's previous fMRI studies of social attribution in healthy adults, which used experimental manipulations that were conceptually similar to the one used in the present study and consistently found robust effects (mean $N = 19$, $SD = 5.67$, range = 10–29; Spunt & Adolphs, 2014; Spunt et al., 2010; Spunt & Lieberman, 2012a, 2012b; Spunt & Lieberman, 2013; Spunt et al., 2011).

Participants in the present study were screened to ensure that they were right-handed, were neurologically and psychiatrically healthy, had normal or corrected-to-normal vision, spoke English fluently, had an IQ in the normal range (as assessed using the Wechsler Abbreviated Scales of Intelligence; Wechsler, 1999), and were not pregnant or taking any psychotropic medications at the time of the study. All participants provided written informed consent according to a protocol approved by the California Institute of Technology Institutional Review Board, and they received financial compensation in exchange for participating.

Procedure

Participants' brain activity was measured while they performed the social/nonsocial *why/how* task, a modified version of the yes/no *why/how* task, which we recently validated for investigating social-attributional processing both behaviorally and neurally (Spunt & Adolphs, 2014). In that study, participants answered attributional (*why*) and factual (*how*) questions about the emotional facial expressions and intentional hand actions depicted in photographs (Fig. 1). This basic protocol of the *why/how* task permits an isolation of the attributional process of interest by allowing researchers to subtract brain activity associated with factual ("how") questions from brain activity associated with attributional ("why") questions. Because each photograph is evaluated using both question types, only the level of attributional processing differs. In this way, the *why/how* manipulation has been used to isolate the brain regions specific to attributional processing in the social domain.

For the present study, we followed three criteria in constructing an orthogonal *why/how* manipulation in the nonsocial domain:

- Stimulus: The stimulus being evaluated does not show humans, human-like entities, or outcomes that are typically the result of intentional human behavior.
- Task content: The attributions that participants are evaluating do not contain the mental and social concepts typically featured in attributions about human behavior.

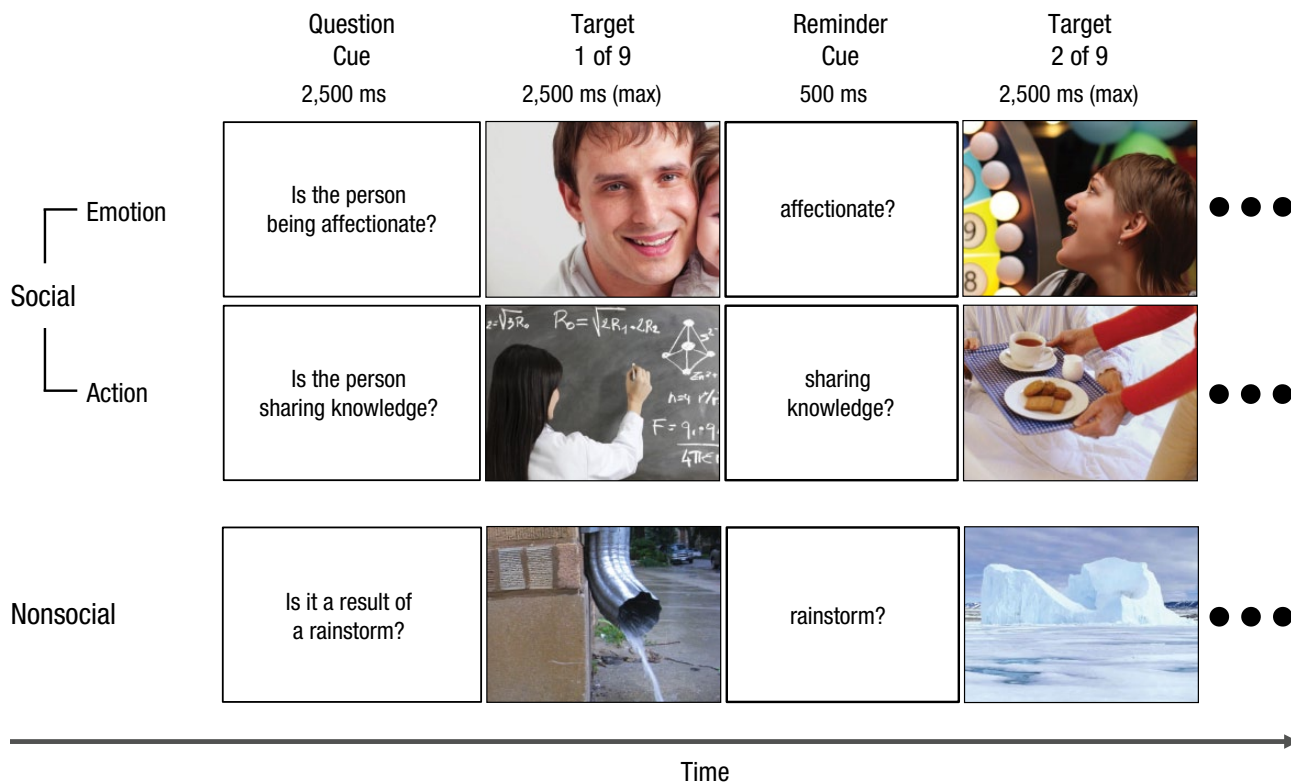


Fig. 1. Sample block sequences from the social/nonsocial *why/how* task. Participants answered yes/no questions about photographs of events that were either social (another person's emotion or action) or nonsocial. Each block began with a yes/no question that was either attributional (it asked participants to consider an explanation of an event) or factual (it asked participants to consider a concrete detail of an event). A sequence of nine photographs followed, with a key phrase from the question appearing as a reminder between photos. For each of these nine photos, participants were instructed to quickly and accurately answer the question presented at the beginning of the block.

- c. Task structure: The task period during which brain activity is measured is structured so as to prevent the occurrence of task-irrelevant social inferences. This criterion is important given the well-documented human tendency to spontaneously anthropomorphize nonsocial objects and events (Epley, Waytz, & Cacioppo, 2007). In fact, the possibility of task-irrelevant social cognition has been used to explain previous findings showing that some nonsocial-reasoning tasks also activate regions involved in social reasoning (Van Overwalle, 2011).

The resulting task featured a 2 (question: *why* vs. *how*) \times 3 (stimulus: nonsocial scenes vs. emotional expressions vs. intentional actions) factorial design. Henceforth, we use the label "social" to collectively refer to the two categories of human behavior (emotional expressions and intentional actions). Each of the three stimulus categories featured 54 naturalistic photographs acquired from a variety of online stock photography sources (see Fig. 1 for examples and Figs. S1–S3 in the Supplemental Material available online for the full stimulus sets). The nonsocial stimuli depicted events

commonly attributed to changes in nature, for instance, extreme weather and seasonal changes. We used Amazon's Mechanical Turk to collect normative ratings of photograph valence from approximately 30 native-English-speaking U.S. citizens. This was achieved by asking participants to rate "How POSITIVE (pleasant) vs. NEGATIVE (unpleasant) is each photo?" on a 7-point Likert scale (1 = *extremely positive*, 4 = *neutral*, 7 = *extremely negative*). An independent samples *t* test showed that photograph valence did not differ significantly across the social ($M = 3.647$, $SD = 0.577$) and nonsocial ($M = 3.731$, $SD = 0.742$) stimulus domains, $t(160) = 0.307$, $p = .759$.

All *why* and *how* questions were in a binary format (the answers required only a "yes" or "no" response). Table 1 displays the 36 questions used in the study. For the social situations, attributional questions regarded the mental state of the person in the photograph (e.g., "Is the person expressing gratitude?"), while factual questions regarded an observable motor behavior (e.g., "Is the person reaching for something?"). For nonsocial situations, attributional questions regarded a natural causal process or occurrence (e.g., "Is it the result of Spring season?"),

Table 1. Question Endings Used in the Social/Nonsocial *Why/How* Task

Stimulus category	Attributional questions (why)	Factual questions (how)
Nonsocial scenes	... Spring season?	... clouds?
	... a drought?	... colorful flowers?
	... a forest fire?	... dry ground?
	... a hurricane?	... moving water?
	... a rainstorm?	... palm trees?
	... result in rain?	... smoke?
Emotional expressions	... being affectionate?	... gazing up?
	... celebrating something?	... looking at the camera?
	... expressing gratitude?	... looking to the side?
	... expressing self-doubt?	... opening their mouth?
	... in an argument?	... showing their teeth?
	... proud of themselves?	... smiling?
Intentional actions	... competing against others?	... carrying something?
	... doing their job?	... lifting something up?
	... expressing themselves?	... putting something on?
	... helping someone?	... reaching for something?
	... protecting themselves?	... using a writing utensil?
	... sharing knowledge?	... using both hands?

Note: For nonsocial scenes, *why* questions began with either “Is it going to result in . . .” or “It is the result of . . .,” whereas all *how* questions began with “Is the photo showing . . .” For both categories of social scene (emotional expressions and intentional actions), both *why* questions and *how* questions began with the string “Is the person . . .”

while factual questions regarded an observable object or event (e.g., “Is the photo showing colorful flowers?”). Each question was paired with five photographs designed to elicit the response “yes” and four photographs designed to elicit the response “no.” These pairings were selected based on the responses of an independent sample of Mechanical Turk respondents. Each pairing was evaluated by approximately 30 native-English-speaking U.S. citizens. We retained only those pairings that elicited a consensus response. An independent-samples *t* test showed that consensus for nonsocial pairs ($M = 92.704\%$, $SD = 6.532$) did not differ significantly from consensus for social pairs ($M = 92.593\%$, $SD = 6.650$), $t(160) = 0.101$, $p = .920$. In our subsequent analysis of participant performance, consensus data were used to code responses as correct or incorrect.

During MRI scanning, photographs were presented to participants in blocks of nine, with each block associated with one of the 36 questions in Table 1. For each block, participants were first shown a question (e.g., “Is the person being affectionate?”), which was followed by a series of nine target photographs. For each of these photographs, participants were instructed to answer the question presented at the beginning of each block. To reduce working memory load, we presented a key word from the question on screen as a reminder (e.g., “affectionate?”) for 500 ms after each photograph except the final one. Participants had 2,500 ms to respond to each photograph. If they responded before 2,500 ms elapsed, they

automatically advanced to the next part of the block. For this reason, block durations were contingent on response times (RTs). However, total task duration was not, as block onsets were fixed. The order and onsets of question blocks were optimized to maximize the efficiency of separately estimating the *why* > *how* contrast for each of the three stimulus categories. This was achieved by generating the design matrices for 1 million pseudorandomly generated designs, and for each, summing the efficiencies of *why* > *how* contrast estimation for the three categories. The most efficient design was retained and used for all participants.

Prior to entering the scanner, participants were told they would be performing a photograph-judgment test in which they would answer yes/no questions about various kinds of photographs. They were then shown two example trials and were invited to ask the experimenter questions if they did not fully understand the task. Finally, they were told that they would have a limited amount of time to respond to each photograph. Immediately prior to performing the task in the scanner, participants performed a brief practice version of the test featuring stimuli not used in the experimental task.

Stimulus presentation and response recording

Stimuli were presented and responses recorded using the Psychophysics Toolbox (Version 3.0.9; Brainard, 1997;

Pelli, 1997) operating in MATLAB (Version 2012a; The MathWorks, Natick, MA). An LCD projector was used to show stimuli on a screen at the rear of the scanner bore that was visible to participants through a mirror positioned on the head coil. Participants were given a button box and made their responses using their right-hand index and middle fingers.

Personality measurement

For the purposes of exploratory individual difference analyses, we asked participants to complete several self-report questionnaires measuring aspects of an individual's motivation and ability to understand other people's behavior. We explored the moderating effect of these measures to add additional constraint on interpreting the nature of effects observed in our primary analyses.

The short form of the Empathy Quotient questionnaire (Wakabayashi et al., 2006; Baron-Cohen & Wheelwright, 2004; $\alpha = .871$) measures the drive to understand and respond appropriately to the internal states of other people (e.g., "I am good at predicting how someone will feel"). The Social Curiosity Scale (Renner, 2006; $\alpha = .885$) measures a general interest in acquiring novel information about other people (e.g., "Other people's life stories interest me"). Items 10 and 11 on the Social Curiosity Scale were deemed inappropriate and were omitted from the study.¹ Finally, participants completed the Attributional Complexity Questionnaire (Fletcher, Danilovics, Fernandez, Peterson, & Reeder, 1986; $\alpha = .929$), which measures the tendency to produce relatively complex and sophisticated explanations of human behavior (e.g., "I really enjoy analyzing the reasons or causes for people's behavior"). Participants also completed the Gossip Functions Questionnaire (Foster, 2004). However, because responses to this questionnaire demonstrated poor reliability (average scale $\alpha = .359$), they were not retained for further analysis.

Image acquisition

All imaging data were acquired at the Caltech Brain Imaging Center using a Siemens Trio 3.0 Tesla MRI scanner outfitted with a 32-channel phased-array head coil. During the social/nonsocial *why/how* task, we acquired 394 T2*-weighted echo-planar image (EPI) volumes (slice thickness = 3 mm, 46 slices, repetition time = 2,500 ms, echo time = 30 ms, flip angle = 85°, matrix = 64 × 64, field of view = 192 mm). Participants' in-scan head motion was minimal (maximum translation = 2.08 mm, maximum rotation = 1.86°). Following this scan, we acquired an additional 386 EPI volumes for each participant while they performed two additional tasks as part of a separate study. Finally, we acquired a high-resolution anatomical

T1-weighted image (1-mm isotropic) and field maps for use in image preprocessing.

Image preprocessing

Images were analyzed using Statistical Parametric Mapping (Version 8; SPM8; Wellcome Department of Cognitive Neurology, London, England) operating in MATLAB. Prior to statistical analysis, each participants' images were subjected to six preprocessing steps. First, the initial two EPI volumes were discarded to account for T1-equilibration effects, and then the remaining EPI volumes were corrected for slice-timing differences. Next, within each run, EPI volumes were realigned to the first EPI volume of the run, and participants' T1 structural volume was coregistered to the mean EPI volume. The group-wise diffeomorphic-anatomical-registration-through-exponentiated-lie registration method included in SPM8 (Ashburner, 2007) was subsequently used to normalize the T1 structural volume to a common group-specific space, with subsequent affine registration to Montreal Neurological Institute (MNI) space. Finally, all EPI volumes were normalized to MNI space using the deformation flow fields generated in the previous step, which simultaneously resampled volumes (3-mm isotropic) and applied spatial smoothing (Gaussian kernel of 8-mm isotropic, full width at half maximum).

Within-subjects contrast estimation

We used a general linear model to estimate the effects of performing the social/nonsocial *why/how* task on the EPI time series for each participant. Each model included six covariates of interest corresponding to the six cells created by crossing factors corresponding to the question (*why* vs. *how*) and stimulus (nonsocial scenes vs. emotional expressions vs. intentional actions) factors. These regressors were defined using a variable-epoch model (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008), with the epochs for each block spanning the onset of the first trial and the offset of the last trial. Each model also included several covariates of no interest. Two parametric covariates of no interest were included that modeled variability in the amplitude of the blood-oxygen-level-dependent response that could be explained by differences in response accuracy and RTs across task blocks (regardless of condition). These covariates were deemed necessary to account for differences in performance that were observed across conditions.

The remaining covariates of no interest included the six motion parameters estimated from image realignment as well as a predictor for every time point during which in-brain global signal change exceeded 2.5 standard deviations of the mean global signal change or during

which estimated motion exceeded 0.5 mm of translation or 0.5 degrees of rotation. The hemodynamic response was modeled using the canonical (double-gamma) response function, and the predicted and actual signals were high-pass-filtered at 1/128 Hz. Finally, all models were estimated using the SPM8 RobustWLS toolbox, which implements the robust weighted least-squares estimation algorithm (Diedrichsen & Shadmehr, 2005).

Group-level analyses

Our primary analyses were conducted at the group level. Given extensive prior work identifying those brain regions most reliably associated with social attribution (Spunt & Adolphs, 2014; Spunt et al., 2010; Spunt & Lieberman, 2012a, 2012b; Spunt et al., 2011), we first tested our group-level hypotheses on a set of independently defined regions of interest (ROI). We focused on six left-hemisphere ROIs that were defined based on the *why* > *how* contrasts reported in Study 1 ($N = 29$) and Study 3 ($N = 21$) of Spunt and Adolphs (2014). These contrast images are publicly available for download on the first author's Web site (<http://bobspunt.com/whyhow-localizer>). ROI sections are depicted in Figure 2a (further details can be found in Table S3 in the Supplemental Material). For each ROI, we extracted percentage signal change (PSC) in the six conditions of the experimental design. To test for domain generality, we used paired-samples *t* tests to identify those regions that independently demonstrated an association with the *why* > *how* contrast for all three stimulus categories. To test for domain-specificity, we used one-sample *t* tests to identify those regions that showed a positive effect in two interaction contrasts: ($[why_{emotions} > how_{emotions}] > [why_{nonsocial} > how_{nonsocial}]$) and ($[why_{actions} > how_{actions}] > [why_{nonsocial} > how_{nonsocial}]$). For each test, we report *p* values corrected for multiple comparisons across ROIs using the false-discovery-rate procedure described in Benjamini and Yekutieli (2001). Confidence intervals (CIs) for these effects were estimated using the bias-corrected and accelerated-percentile method (10,000 random samples with replacement; implemented using the BOOTCI function in MATLAB).

ROI analyses were followed by whole-brain analyses. To determine the extent to which the *why* > *how* contrast isolates regional activation that is domain general, we subjected the contrast images for each stimulus category to one-sample *t* tests and used the resulting *t*-statistic images to compute the minimum *t*-statistic image required for valid conjunction inference (Nichols, Brett, Andersson, Wager, & Poline, 2005). Next, two interaction-contrast images were computed, one indexing the relative strength of the *why* > *how* effect for emotional expressions compared with

nonsocial scenes ($[why_{emotions} > how_{emotions}] > [why_{nonsocial} > how_{nonsocial}]$) and one indexing the relative strength of the *why* > *how* effect for actions compared with nonsocial scenes ($[why_{actions} > how_{actions}] > [why_{nonsocial} > how_{nonsocial}]$). To determine the extent to which the *why* > *how* contrast isolates a response that is selective for the social domain, we subjected the contrast images for each interaction to one-sample *t* tests and used the resulting *t*-statistic images to compute the minimum *t*-statistic image. This conjunction isolates regions that show a stronger response to the *why* > *how* contrast for both emotional expressions and intentional actions relative to nonsocial scenes. Whole-brain analyses were conducted by applying a cluster-forming (voxel-level) threshold of $p < .001$ followed by cluster-level correction for multiple comparisons at a family-wise-error rate of .05. For visual presentation, thresholded *t*-statistic maps were overlaid on the average of the participants' T1-weighted anatomical images.

Individual difference analyses

For each participant, MATLAB was used to score and assess the reliability of responses to the personality measures and to compute measures of mean percentage accuracy and RT for the social/nonsocial *why/how* task. Prior to computing accuracy, we omitted trials with no response, which were rare (across participants, $M = 0.97\%$, $SD = 1.94\%$, maximum value for individual participants = 8.33%). To address negative skewness, we subjected accuracy scores to a Box-Cox transformation (Box & Cox, 1964). Mean RT was computed on the distribution of correct trials only and after deleting values that were greater than 3 standard deviations from the remaining distribution mean. (Group-level descriptive statistics are reported in Table S1 in the Supplemental Material.)

To examine brain-behavior relationships, we computed each participant's mean PSC within the dorso-medial prefrontal cortex (DMPFC) ROI in each domain's *why* > *how* contrast. Then, we used the MATLAB Statistics Toolbox to perform a series of robust multiple regression analyses that simultaneously modeled the influence of DMPFC responses to the two domains on five outcomes of interest: attributional accuracy in the social and nonsocial domains,² and the three personality measures (Empathy Quotient questionnaire, Social Curiosity Scale, and Attributional Complexity Questionnaire). Robust regressions were carried out using iteratively reweighted least squares estimated as implemented in the MATLAB Statistics Toolbox. (Zero-order Pearson correlations among all examined variables are reported in Table S6 in the Supplemental Material.)

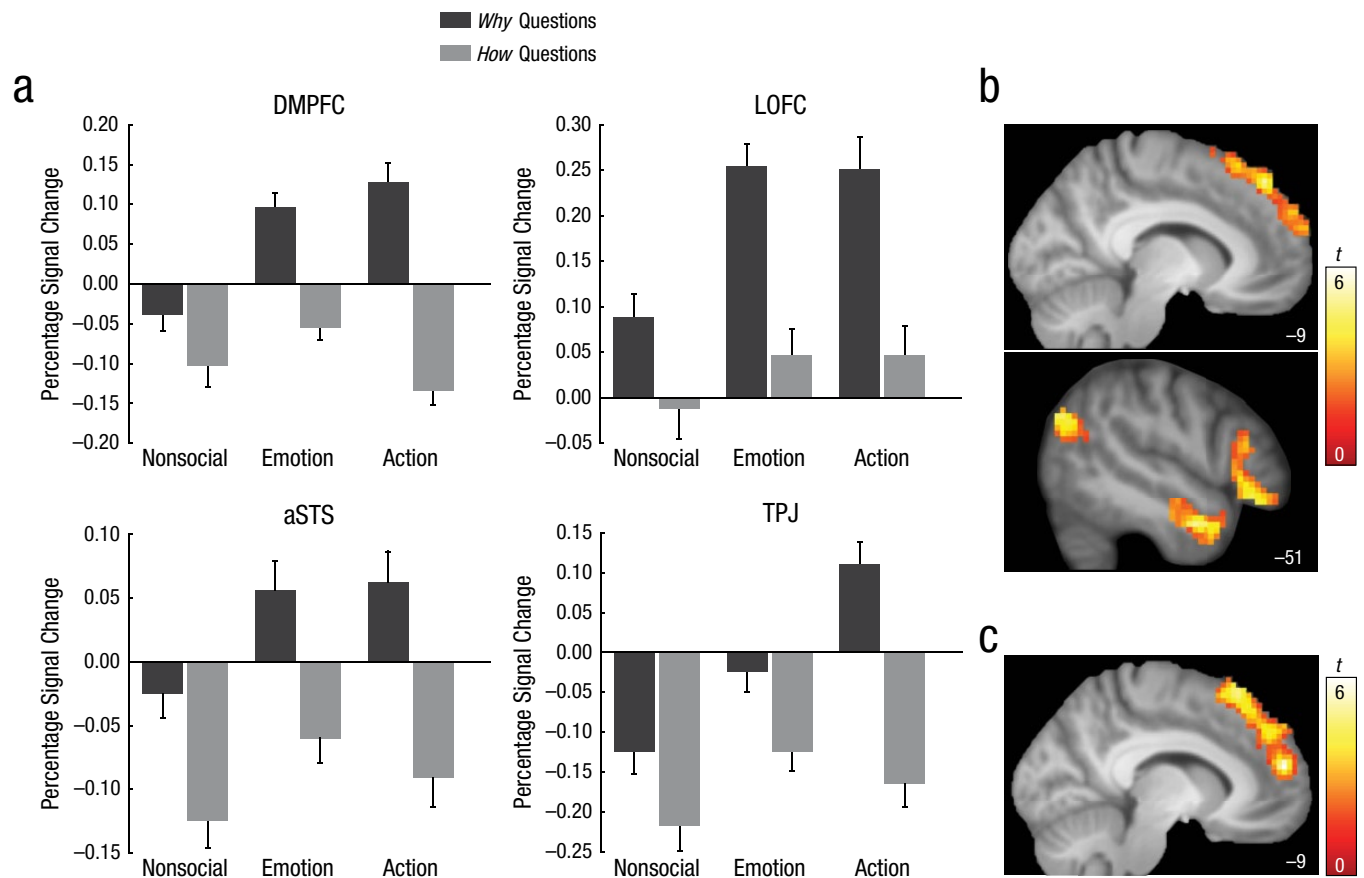


Fig. 2. Results from the region-of-interest (ROI) and whole-brain analyses. The graphs in (a) show mean percentage signal change from fixation baseline as a function of stimulus category and question type, separately for each of the independently defined ROIs that showed an association with the *why* > *how* contrast for all three stimulus categories (nonsocial scenes, emotional expressions, intentional actions). The sagittal slices in (b) and (c) illustrate the results of whole-brain analyses. In (b), the images show regions independently associated with the *why* > *how* contrast for all three stimulus categories. The image in (c) shows the portion of the dorsomedial prefrontal cortex (DMPFC) that displayed an elevated response in the *why* > *how* contrast to attributions about both emotional expressions and intentional actions compared with attributions about nonsocial situations. For both whole-brain analyses, regions were identified from a group-level ($N = 19$) search using a cluster-forming threshold of $p < .001$ and a cluster-level family-wise-error rate of .05. Activity is overlaid on the group mean anatomical map at a threshold of $p < .005$ to show the extent of activation. LOFC = lateral orbitofrontal cortex; aSTS = anterior superior temporal sulcus; TPJ = temporoparietal junction.

Results

Domain-general effects

As displayed in Figure 2a, four of the six ROIs examined demonstrated evidence of a domain-general association with the *why* > *how* contrast (see also Table S4 in the Supplemental Material). These were the DMPFC, the lateral orbitofrontal cortex (LOFC), the aSTS, and the TPJ. As displayed in Figure 2b and listed in Table 2, activations in each of these regions were also observed in whole-brain analyses based on the conjunction of the *why* > *how* contrast for the three stimulus categories. While these findings still leave open the possibility of representational differences within the observed regions in the way that social and nonsocial attributions correspond with brain-activation patterns (as could be revealed

through pattern-information analysis, e.g., Kriegeskorte & Kievit, 2013), they argue strongly for a broadly similar set of psychological processes engaged in both cases.

Effects specific to the social domain

The results for domain-general effects thus suggest that many of the brain regions associated with the *why* > *how* contrast in the social domain are also associated with that contrast in the nonsocial domain. In our next analysis, we sought to identify those regions demonstrating evidence of a response to attributional processing that is specific to the social domain. To do so, we capitalized on the fact that we operationally defined the social domain in two ways: using photographs of emotional facial expressions and photographs of intentional hand actions. For a region

Table 2. Results of Group-Level Whole-Brain Conjunction Analyses

Region	Hemisphere	Number of voxels	<i>t</i> (18)	MNI coordinates		
				<i>x</i>	<i>y</i>	<i>z</i>
Response to <i>why</i> > <i>how</i> questions for all stimulus categories						
Anterior superior temporal sulcus	Left	124	5.837	−57	0	−21
Dorsomedial prefrontal cortex	Left	69	5.376	−9	45	51
Lateral orbitofrontal cortex	Left	92	5.148	−48	33	−12
Lateral orbitofrontal cortex	Left	—	4.153	−45	24	15
Temporoparietal junction	Left	59	5.043	−51	−69	33
Temporoparietal junction	Left	—	4.539	−42	−51	21
Stronger response to <i>why</i> > <i>how</i> questions for social than for nonsocial stimuli						
Dorsomedial prefrontal cortex	Left	303	6.245	−9	57	18
Dorsomedial prefrontal cortex	Left/Right	—	5.942	0	51	36
Dorsomedial prefrontal cortex	Left	—	5.346	−9	29	58
Dorsomedial prefrontal cortex	Right	—	4.649	12	57	12

Note: *N* = 19. The minimum statistic image was cluster-corrected at a family-wise-error rate of .05. MNI = Montreal Neurological Institute.

to be characterized as functionally sensitive to the social domain, it should demonstrate this sensitivity in response to both emotions and actions. To identify such regions, we examined the conjunction of two interaction contrasts: ($[why_{emotions} > how_{emotions}] > [why_{nonsocial} > how_{nonsocial}]$) and ($[why_{actions} > how_{actions}] > [why_{nonsocial} > how_{nonsocial}]$). Although every ROI except for the aSTS displayed an elevated response to at least one of the two social-stimulus categories (Table S5 in the Supplemental Material), only the left DMPFC showed an elevated response to both social-stimulus categories, and did so both in ROI and in whole-brain analyses (Fig. 2c; Table 2). That is, although largely the same area of the DMPFC demonstrated a domain-general association with making attributions, this association was stronger for attributions made about social situations than about nonsocial situations.

Dispositional moderators of DMPFC responses

To provide further constraints on interpreting the nature of the elevated DMPFC response to social attributions, we capitalized on individual variability in performance both on the social- and nonsocial-attribution tasks, as well as in self-reported personality traits relevant to social cognition. We used these factors to rule out a potent alternative interpretation of the domain-general effects observed in this region. That is, activation of the DMPFC in the nonsocial *why* > *how* contrast may be caused by task-irrelevant social-attributional processing that may occur spontaneously during performance of the nonsocial-attributional task. This interpretation has been used before to explain observations of DMPFC activation in

nonsocial-reasoning tasks (Van Overwalle, 2011) and is made especially viable given the strong human tendency to anthropomorphize nonsocial objects and events (Epley et al., 2007). Moreover, this could also account for the fact that the DMPFC response to nonsocial attributions was globally weaker when compared with its response to social attributions.

To evaluate this possibility, we tested two hypotheses. First, if DMPFC function is irrelevant to the nonsocial-attribution task, individual differences in the level of DMPFC activation to nonsocial attributions should be either uncorrelated or negatively correlated with levels of performance on the nonsocial-attribution task. Such an effect would be consistent with the well-established association of the DMPFC with mind wandering, stimulus-independent thought, and the default-mode network of the brain more broadly (Mason et al., 2007). If instead the DMPFC is critical to performance of the nonsocial-attribution task, its levels of activation in response to the nonsocial domain should be positively associated with making more accurate attributions in that domain. Moreover, this association should be evident even when accounting for the DMPFC response to attributions in the social domain.

To evaluate these alternatives, we used multiple regression to simultaneously model the influence of domain-specific DMPFC activation and attributional accuracy in both domains (results are shown in Table 3, with zero-order correlations provided in Table S6). The results strongly support the proposition that the DMPFC association with attributional processing is domain general: DMPFC activation to the nonsocial (but not social) domain was uniquely associated with attributional accuracy in the

Table 3. Results of Robust Multiple Regression Analyses of Domain-Specific Activation in the Dorsomedial Prefrontal Cortex (DMPFC) as a Predictor of Individual Difference Outcomes

Outcome predicted	Nonsocial domain			Social domain		
	β	$t(16)$	p	β	$t(16)$	p
Accuracy: nonsocial attribution	0.55 [0.11, 0.99]	2.65	.017	0.24 [-0.20, 0.69]	1.17	.260
Accuracy: social attribution	0.14 [-0.26, 0.54]	0.75	.466	0.67 [0.27, 1.07]	3.56	.003
Empathy	-0.37 [-0.78, 0.05]	-1.86	.081	0.59 [0.18, 1.01]	3.02	.008
Social curiosity	-0.14 [-0.56, 0.27]	-0.73	.474	0.69 [0.28, 1.11]	3.52	.003
Attributional complexity	-0.30 [-0.74, 0.14]	-1.44	.170	0.62 [0.18, 1.06]	3.01	.008

Note: All five regression models contained the same two predictors: DMPFC activation to the *why* > *how* contrast in the nonsocial domain, and DMPFC activation to the *why* > *how* contrast in the social domain. Values in brackets are 95% confidence intervals. The DMPFC region was defined using the same region of interest used to examine within-subjects effects.

nonsocial domain, while the DMPFC activation to the social (but not nonsocial) domain was uniquely associated with attributional accuracy in the social domain. This evidence argues against the possibility that the domain-general effects observed in the DMPFC are simply a by-product of incidental processing shared across the domains.

If the DMPFC response to nonsocial attribution were to reflect spontaneous social cognition, a second prediction would be that this task-irrelevant response should be strongest in those individuals most inclined to show spontaneous social cognition. Indeed, Wagner, Kelley, and Heatherton (2011) recently showed that individual differences in task-irrelevant DMPFC responses to social scenes positively correlate with scores on the Empathy Quotient questionnaire. Similarly, we found that DMPFC responses to social attributions in our task were uniquely positively associated not only with scores on the Empathy Quotient questionnaire, but also with self-reported measures of social curiosity and attributional complexity (Table 3). In contrast, the DMPFC response to nonsocial attribution demonstrated no unique association with these measures. Hence, though the DMPFC response to nonsocial attribution was generally weaker than its response to social attribution, these secondary analyses strongly suggest that it nonetheless comes into play during both kinds of attributions and, moreover, does so as a function of the relative expertise and performance abilities of each participant with respect to that domain of attribution.

Discussion

We observed that most of the brain regions activated by social attributions were also activated by nonsocial attributions. Moreover, individual differences in the domain-specific recruitment of one of these regions—the DMPFC—correlated with attributional accuracy in each domain. DMPFC also showed an elevated response to attributions about social situations, and this socially

selective response was strongest in those participants who reported the highest levels of social expertise. On the basis of these findings, we suggest that attributions about the social world reflect a specialized use of a domain-general cognitive ability.

The regions associated with attributional processing in the present study are anatomically similar to those observed in neuroimaging studies of social reasoning (Amodio & Frith, 2006; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Van Overwalle & Baetens, 2009). Given proposals that these regions may implement processes that are dedicated to social cognition (Kennedy & Adolphs, 2012; Mitchell, 2009; Van Overwalle, 2011), it may be surprising that these regions demonstrated an association with attributions about nonsocial situations. We believe this apparent discrepancy with prior research is explained by several distinctive features of the present study's methods.

First, we used a factorial design to independently manipulate attributional processing (*why* vs. *how* questions) and stimulus domain (social vs. nonsocial scenes). This allowed us to conduct independent tests for attribution-specific brain activity within each domain. Previous researchers either could not or did not conduct such tests and instead relied on directly comparing brain activity elicited by judgments of social and nonsocial stimuli (e.g., Martin & Weisberg, 2003; Mason et al., 2010; Mitchell et al., 2002; Mitchell et al., 2005). As the present findings suggest, brain activity observed in such direct comparisons could be caused by social and nonsocial stimuli placing different demands on the same cognitive process.

Second, normative data allowed us to assess the accuracy of participants' attributional judgments. This data, in turn, allowed us to demonstrate that, in addition to showing a domain-general association with attributional processing, DMPFC activity also shows a domain-general association with attributional accuracy. This degree of experimental control over both stimulus and response was largely absent from previous neuroimaging studies

comparing social and nonsocial reasoning (Baetens, Ma, Steen, & Van Overwalle, 2014; Mitchell et al., 2005). Given that people spontaneously generate social interpretations of nonsocial stimuli (Epley et al., 2007), it is difficult to interpret brain activity associated with nonsocial reasoning during tasks in which participant responses are unconstrained or unmeasured.

Finally, we acknowledged that the social world is heterogeneous and therefore operationally defined it with two distinct classes of human behavior: emotional expressions and intentional actions. The importance of this is demonstrated by the fact that several regions showed a socially selective response to attributions about either emotions or actions, but not to both (see Table S5). This strengthens the conclusion that the DMPFC is selective for the abstract domain shared by emotions and actions, namely, the social domain.

What domain-general process could implement social attributions? One answer emerges from neuroimaging studies of semantic-memory use (Binder & Desai, 2011). In a meta-analysis of 120 fMRI studies, Binder, Desai, Graves, and Conant (2009) identified a network that includes the set of regions that showed a domain-general association with attribution in the present study. Other reviews and meta-analyses have identified similar anatomical correspondences across mental-state reasoning tasks and task groups with strong semantic-memory demands, for instance, narrative comprehension, prospection, and autobiographical memory (Mar, 2011; Schacter et al., 2012; Spreng, Mar, & Kim, 2009). Such data fit with a view of folk attribution as heavily dependent on the efficient retrieval, selection, and integration of semantic memory, that is, world knowledge that is not reliably tied to observable objects and events (Fletcher et al., 1986). Hence, social and nonsocial attribution appear to be isomorphic uses of semantic memory, in that both demand comprehending the contents of a visual scene (e.g., smiling face, blooming flower) using relatively abstract causal schemata (e.g., friendliness, Spring season).

The plausibility of this domain-general view depends on its ability to account for the socially selective response of the DMPFC to attributional processing. Our individual-differences analyses provide valuable constraint on interpreting this effect. First, although nonsocial attributions elicited modest DMPFC response across participants, individual differences in the magnitude of this response nevertheless uniquely correlated with attributional accuracy in the nonsocial domain. Second, individual differences in responses to social attribution were uniquely associated not only with attributional accuracy in the social domain, but also with self-reported levels of empathy, social curiosity, and attributional complexity. In other words, those individuals who demonstrated the greatest

ability in a given domain also tended to show the strongest DMPFC responses to that domain.

To accommodate these findings, a semantic-memory account need assume only that most people are substantially interested in and knowledgeable about the causal factors at play in their social worlds. Such depth of domain-specific knowledge would be predicted to place strong demands on the executive aspects of semantic-memory use that includes the retrieval, selection, and integration of conceptual knowledge. Regions of the DMPFC have been linked with these functions in both nonsocial and social semantic-memory tasks (Binder & Desai, 2011; Binder et al., 2009; Goel, Gold, Kapur, & Houle, 1997; Jenkins & Mitchell, 2010; Mitchell, 2009; Satpute, Badre, & Ochsner, 2014). Moreover, neuroimaging studies of social reasoning indicate that the DMPFC plays a central executive role in the use of social knowledge (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012; Spunt & Lieberman, 2013). Hence, in the same way that the face-selective response of the fusiform face area may be explained by acquired perceptual expertise (Tarr & Gauthier, 2000), the socially selective response of the DMPFC during attributional processing may be best explained by conceptual expertise acquired as a natural consequence of living in a world that is thoroughly and inescapably social (Barrett & Satpute, 2013; Fiske & Taylor, 1984; Fletcher et al., 1986; Grelotti et al., 2002; Roy, Shohamy, & Wager, 2012). Future studies will be needed to evaluate additional predictions of a conceptual-expertise account of attributional processing. For instance, DMPFC selectivity for the social domain should be atypical in psychiatric conditions that severely impede the acquisition of social expertise (Grelotti et al., 2002; Kennedy & Adolphs, 2012). In fact, work is currently being conducted in our lab to investigate this possibility in a group of high-functioning adults with autism. A second prediction regards acquired expertise in (nonsocial) knowledge domains, for instance medicine. In such cases, DMPFC selectivity for attributions within that domain should parametrically track individual differences in domain-specific experience (e.g., year in medical school) and performance (e.g., diagnostic accuracy).

The present study suggests that social attributions rely on a process, possibly centralized in the DMPFC, that can be used to make attributions about nonsocial situations. By showing only this, our findings remain consistent with proposals that the basic cognitive mechanisms supporting social reasoning evolved specifically in response to the increasing complexity of primate social structures (Cosmides & Tooby, 1992; Dunbar, 1998; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007) and later were repurposed for use in other domains. In fact, the complexity and heterogeneity of the social world may be

the very reason why this ability can be flexibly repurposed for use in other domains.

Indeed, Herrmann and colleagues (2007) reached a similar conclusion in a study comparing the social and nonsocial cognitive skills of 2.5-year-old human children with those of chimpanzees. While the children generally outperformed the chimpanzees in the social but not the nonsocial domains, there was one nonsocial skill area in which the children excelled: causal understanding. On the basis of this finding, Herrmann and colleagues speculate that “what is distinctively human is not social-cultural cognition as a specialized domain, as we have hypothesized. Rather, what may be distinctive is the ability to understand unobserved causal forces in general, including (as a special case) the mental states of others as causes of behavior” (p. 1365). While the findings presented here support such a “special case” perspective on social-causal attribution, they suggest that of all the possible uses humans have for this ability, its use in understanding the social world is the most important.

Author Contributions

R. P. Spunt and R. Adolphs designed the study and created the analytical strategy, R. P. Spunt collected and analyzed the data, and both authors wrote the manuscript.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information can be found at <http://pss.sagepub.com/content/by/supplemental-data>

Open Practices



All materials have been made publicly available via Open Science Framework and can be accessed at <https://osf.io/59cbe>. Group-level statistical contrast images can be downloaded as a NeuroVault collection: <http://neurovault.org/collections/297/>. The complete Open Practices Disclosure for this article can be

found at <http://pss.sagepub.com/content/by/supplemental-data>. This article has received a badge for Open Materials. More information about the Open Practices badges can be found at <https://osf.io/tyvzx/wiki/view/> and <http://pss.sagepub.com/content/25/1/3.full>.

Notes

1. Both items can be interpreted as references to a stereotypical stalking behavior: “I like to stand at the window and watch what my neighbors are doing” (Item 10) and “I like to look into other people’s windows” (Item 11). Excluding these items did not substantively change the results.
2. Given that DMPFC activity was theorized to be functionally relevant for answering only *why* questions, attributional accuracy was defined by the percentage of correct responses to *why* questions. The validity of the *why* > *how* accuracy difference depends on an assumption we were not prepared to make, namely, that accuracy and DMPFC activity during *how* questions will have a negative association that is as strong as the predicted positive association between accuracy and DMPFC activity during *why* questions.

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